Population dynamics of the northern short-tailed shrew, Blarina brevicauda: insights from a 25-year study

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Population dynamics of the northern short-tailed shrew, Blarina brevicauda: insights from a 25-year study

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Abstract: Population demography of the northern short-tailed shrew, Blarina brevicauda, was studied for 25 years in bluegrass, alfalfa, and tallgrass habitats in east-central Illinois. The population in bluegrass had higher over-winter population density, began increasing earlier in the year, peaked earlier in the year, had higher mean monthly population densities and amplitudes of fluctuation, and remained higher longer than did populations in alfalfa and tallgrass. Survival rates and persistence were greater in bluegrass and tallgrass than in alfalfa. The species displayed annual population fluctuations with little variation in amplitude among years in all three habitats. Seasonal reproduction appeared responsible for the annual fluctuations. Survival did not vary in relation to season, but was positively correlated with annual peak densities whereas reproduction was not. There was no correlation between population densities of voles during April-August and annual peak densities of B. brevicauda. We conclude that annual fluctuations in B. brevicauda are driven by seasonal reproduction, while variation in mortality, most likely from predation, may explain differences in the amplitudes of annual peaks.

Introduction

Although the short-tailed shrew, Blarina brevicauda, is one of the more common small mammals in eastern North America, there are relatively few long-term demographic studies of the species (Getz 1989, 1994). High trap mortality (Blair 1940; Getz 1961) or use of snap- or pitfall-trapping (Pankakoski 1985), combined with typically short-term field studies, result in too few data for adequate demographic analyses. During the course of a 25-year study of the prairie vole, Microtus ochrogaster, and meadow vole, M. pennsylvanicus, in east-central Illinois (Getz et al. 2001), data concerning B. brevicauda were also collected in three habitat types: alfalfa, bluegrass, and tallgrass prairie. While trap mortality of shrews also was high in our study, the data obtained were sufficient for analysis of many aspects of the demography of the species. Most species that prey on voles also take B. brevicauda (Bent 1937, 1938; Whitaker and Hamilton 1998). Both species of voles underwent erratic high amplitude fluctuations in population densities in our study sites (Getz et al. 2001). If predation were a major factor in the demography of B. brevicauda, we would expect high amplitude fluctuations of B. brevicauda that are in synchrony with those of voles in the same sites. B. brevicauda has been reported to display either annual or irregular fluctuations in population density (Harper 1929; Blair 1940, 1948; Manville 1949; Buckner 1966; Smith et al. 1974; Grant 1976; Yahner 1983; Lima et al. 2002). Further, preliminary analyses of the first 18 years of this study (Getz 1989, 1994) indicated that B. brevicauda displayed annual fluctuations, with little year-to-year variation in peak densities. Blarina brevicauda has been proposed as a predator on arvicoline rodents (Eadie 1944, 1948, 1952). Although the ability of B. brevicauda to kill free-living adult voles has been questioned by Barbehenn (1958) and Lomolino (1984), the latter suggested the species to be an important predator on juvenile M. pennsylvanicus. Getz et al. (1992) concluded from studies in semi natural environments that B. brevicauda might be an important predator on M. pennsylvanicus nestlings, but not on M. ochrogaster nestlings. If such findings can be applied to the field, then we might expect the population densities of M. pennsylvanicus and B. brevicauda to affect one another. Blarina brevicauda has high water requirements (Chew 1951) and is associated with mesic habitats (Pruitt 1953, 1959; Getz 1961). Population demography of B. brevicauda in drier habitats would be expected to be influenced by variation in precipitation. Matlack et al. (2002) found a correlation between precipitation and population densities of Blarina hylophaga. Smith et al. (1974) suggested precipitation the prior autumn to have an impact on shrew population densities the following year.

We used Blarina brevicauda data from the entire 25 years of the study to test the following predictions: (1) the species displays annual rather than multi-annual population fluctuations, (2) population densities and annual peaks are higher during years of high precipitation, and (3) population densities are correlated with those of M. pennsylvanicus, but not M. ochrogaster.

Study sites and procedures

Study sites

The study sites were located in the University of Illinois Biological Research Area ("Phillips Tract") and Trelease Prairie, both 6 km NE of Urbana, Illinois (40°15'N, 88°28'W). Populations of B. brevicauda were monitored in three distinct habitats from 1972-1997: bluegrass, Poa pratensis, alfalfa, Medicago sativa, and restored tallgrass prairie. Getz et al. (1987, 2001) provided detailed descriptions of the study areas; only brief descriptions are given here.

Vegetative cover was most dense in bluegrass and least so in alfalfa. Vegetative cover, including a mat of dead grass litter, 5-25 cm above the surface was very dense throughout the year in bluegrass; B. brevicauda made use of vole surface runways through the vegetation and litter. Larger forbs provided considerable cover up to 1-2 m above the surface during summer-late autumn. Vegetative cover in alfalfa was more dense from mid spring through early winter, than during late winter-early spring when much of the surface was exposed. During mid spring-early winter, alfalfa plants were less than 0.5 m tall and there were only scattered taller plants providing cover up to 1.0 m above the surface. Vegetative cover in tallgrass was dense throughout the year. During spring-early summer, grasses formed cover 0.5-1.0 m high; from late summer-early winter, there was dense vegetative cover 1.0-1.5 m above the surface. During the entire year, recumbent dead grasses formed a dense layer approximately 25 cm above the surface. Owing to

the bunch growth-form of the tall grasses, the area between the bases of tall grass clumps was relatively open up to 10 cm above the surface at all times.

All study sites, except for a small (≈ 0.1 ha) area in the Trelease tallgrass site (trapped only 1972-1977), were well-drained and relatively dry except following heavy rains. Weather data were compiled from the Illinois State Water Survey climatological data records. The weather station was located on the campus of the University of Illinois, approximately 10 km SW of the study sites.

Trapping procedures

A grid system with 10-m intervals was established in all study sites. One wooden multiple-capture live-trap (Burt 1940) was placed at each station. Each month a 2-day prebaiting period was followed by a 3-day trapping session. Because the study was designed for voles, cracked corn was used for prebaiting and as bait in the traps. Cracked corn is not a suitable food for shrews. We used vegetation or aluminum shields to protect the traps from the sun during the summer. The wooden traps provided ample insulation in the winter so nesting material was not placed in the traps at any time. Traps were set in the afternoon and checked at approximately 0800h and 1500h the following 3 days. All live shrews were toe-clipped at first capture for individual identification (maximum of 2 toes on each foot). The field protocol was reviewed periodically by the University of Illinois Laboratory Animal Resource Committee throughout the study and approved, based on University and Federal guidelines, as well as those recommended by the American Society of Mammalogists, in effect at the time.

Data analysis

Of the 7,203 individuals captured during the study, 1,933 (26.8%) were dead at first capture. Another 957 were found dead in traps at subsequent captures, for a total trap mortality of 40.1%. While obviously having an impact upon the populations, trap mortality did not appear to disrupt overall dynamics of our study population or unduly bias our conclusions. B. brevicauda did not enter traps until at least three-fourths grown so we could not distinguish young animals from small adults; thus, we did not separate our data by age class. Estimates of population density were compiled manually, based on the minimum number known alive method (Krebs 1999). Owing to very few captures for many months, often 1 or 2, or no captures at all, and few repeated captures, other models of estimating population density were not appropriate. Population data from all sites within each habitat (Getz 1994) were combined for analysis. Thus, population densities represent averages for all sites within each habitat.

Survival rates were calculated as the proportion of individuals present one month that were trapped the subsequent month. We calculated persistence on the study site as the time elapsed from first capture to disappearance from the site. An animal was presumed to have been present in the site, one half month prior to first capture and persisted one half month following the last capture. We could not distinguish between mortality and emigration in either the monthly survival or persistence analyses.

Owing to difficulty in determining sex and reproductive condition of B. brevicauda from external examination we did not record sex or reproductive condition of most live animals. Reproductive condition was recorded from live males with enlarged testes and from females that were obviously pregnant (confirmed by palpation) or lactating (enlarged nipples). Most reproductive data came from necropsy of animals dead in the traps. Males were recorded as reproductive if the testes were > 3mm in length; females were recorded as reproductive if the uteri were > 2mm in diameter or embryos were present.

Seasonal analyses were based on the following periods: spring (March-May), summer (June-August), autumn (September-November), and winter (December-February). Comparisons of effects of precipitation on peak densities were grouped as to periods with greatest potential for impact: September-December of the previous year and April-August of the same year. April-August is the period of maximum population growth most years.

We examined correlations between (1) January-March B. brevicauda population densities and peak densities that year, (2) April-August vole densities and B. brevicauda peak densities (typically the period during which vole reproduction was greatest and thus nestling voles would be most available as a food source for B. brevicauda), (3) total precipitation the previous September-December and for April-August of the same year and B. brevicauda peak densities, (4) mean monthly survival rates during April-August and peak densities, (5) total precipitation April-August

and mean monthly survival rates, and (6) proportion reproductive April-August and peak densities, and (7) April-August precipitation and proportion reproductive.

Statistical analyses

Because most of the variables used in our analyses did not meet the requirements for normality (population densities and demographic variables were non normal at the 0.05 level; Kolmogorov-Smirnov test, Zar 1999), all variables were log-transformed so we could use parametric analysis of variance (ANOVA) or Pearson's correlation analysis. Significant one-way ANOVAs were followed by Tukey's honestly significant difference (HSD) post-hoc multiple comparisons for significance at $\alpha = 0.05$. We used SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) for the above statistical analyses. Chi square tests, with Yates Correction, were also employed.

Results

Population densities

Mean monthly population densities of B. brevicauda in bluegrass, alfalfa, and tallgrass were 10.3 + 0.5/ha, 6.9 + 0.5/ha, and 5.2 + 0.3/ha, respectively, and differed among habitats ($F[2,881] = 48.302$, $P < 0.001$). Densities in bluegrass were significantly higher than those in alfalfa and tallgrass (Tukey's HSD, $P < 0.05$); differences between alfalfa and tallgrass were not significant ($P > 0.05$).

Blarina brevicauda densities displayed annual fluctuations in all three habitats (Fig. 1). Mean annual peak densities were: bluegrass: 24.2 + 1.9/ha, alfalfa: 20.9 + 1.5/ha, tallgrass, 16.2 + 1.3/ha and differed among habitats ($F[2,72] = 5.219$, $P = 0.008$). Only the difference between bluegrass and tallgrass was significant (Tukey's HSD, $P < 0.05$). The amount of deviation from the mean annual peak density did not differ among the three habitats (7.7 + 1.0/ha, 5.9 + 0.8/ha and 5.1 + 0.8/ha, in bluegrass, alfalfa, and tallgrass, respectively; $F[2,72] = 1.440$, $P = 0.244$). The only significant difference in mean amplitudes of fluctuation among habitats was lower amplitudes (annual low to peak density) in tallgrass than in the other two habitats (21.9 + 1.7/ha, 21.8 + 2.0/ha and 15.5 + 1.4/ha for bluegrass, alfalfa, and tallgrass, respectively; $F[2,72] = 4.331$, $P = 0.017$; Tukey's HSD test, $P < 0.05$).

The overall annual fluctuation varied among habitats (Fig. 2). Population density increased rapidly in both bluegrass and alfalfa, beginning in May, while increases in tallgrass were more gradual and began later (Fig. 2). On average, population density reached the annual peak in July in bluegrass, and in October in both alfalfa and tallgrass ($F[2,72] = 4.234$, $P = 0.018$); only the difference in the month of peaks in bluegrass and tallgrass was significant (Tukey's HSD, $P < 0.05$). Densities in bluegrass declined gradually from the peak through December, before dropping rapidly to a low in March. Population densities in both alfalfa and tallgrass dropped rapidly from the October peak to a low in March.

Population densities declined to zero for at least one month each year during 20 years in alfalfa, 15 years in tallgrass, and only 3 years in bluegrass. Mean monthly population densities during the three months of lowest densities (January-March; Fig. 2) were 4.4 + 0.6/ha, 1.7 + 0.3/ha, and 2.0 + 0.2/ha, in bluegrass, alfalfa and tallgrass, respectively ($F[2,71] = 14.357$, $P < 0.001$). January-March densities in bluegrass were significantly higher than those in alfalfa and tallgrass; there was no difference between alfalfa and tallgrass (Tukey's HSD, $P > 0.05$).

Survival

Monthly survival rates for the entire 25 years were significantly lower in alfalfa than in bluegrass and tallgrass (0.331 + 0.024, 0.466 + 0.014, and 0.398 + 0.022, respectively; $F[2,33] = 10.760$, $P < 0.001$). There was no difference between bluegrass and tallgrass (Tukey's HSD, $P > 0.05$). Mean monthly survival was slightly higher in bluegrass than the other two habitats during all months, except February, July and August, when survival was highest in tallgrass (Table 1). Survival did not differ seasonally within the three habitats (Table 1; alfalfa, $F[3,8] = 0.811$, $P = 0.522$; bluegrass, $F[3,8] = 0.208$, $P = 0.888$; tallgrass, $F[3,8] = 3.207$, $P = 0.083$).

Survival curves for the three habitats indicated higher survival in bluegrass than in alfalfa and tallgrass (Fig. 3). There was no difference in survival among the three habitats the first month following first capture ($\chi 2 = 3.31$, $df = 2$, $P > 0.05$). Survival was significantly greater in bluegrass than in alfalfa and tallgrass the following three months (second month: $\chi 2 = 9.76$, $df = 2$, $P < 0.02$; third month: $\chi 2 = 14.32$, $df = 2$, $P < 0.01$; fourth month: $\chi 2 = 26.13$, $df = 2$, $P < 0.01$). Thereafter the numbers involved were too few for comparisons.

Persistence

Mean persistence in the three habitats, combined, was 1.69 months (n = 5,270). Only 2.1% of the 5,270 animals persisted for six months; six individuals remained for 12 months. Mean persistence times were 1.75 months (N = 3,416), 1.56 months (n = 1,104), and 1.66 months (N = 750) for bluegrass, alfalfa, and tallgrass, respectively ($F[2,5266] = 4.765$ $P = 0.009$). Persistence in bluegrass was greater than that in alfalfa and tallgrass (Tukey's HSD test, $P < 0.05$); there was no difference in persistence in the latter two habitats ($P > 0.05$).

Reproduction

Overall, the proportions of males and females that were reproductive tended to be less in tallgrass than in either bluegrass (males: $\chi 2 = 4.484$, $P = 0.05$; females: $\chi 2 = 13.382$, $P < 0.01$) or alfalfa (males: $\chi 2 = 18.964$, $P < 0.01$; females: $\chi 2 = 12.383$, $P < 0.01$); proportion of reproductive males and females was similar in the two latter habitats (males: $\chi 2 = 2.721$, $P > 0.05$; females: $\chi 2 = 1.089$, $P > 0.05$). There was a tendency for fewer males and females to be reproductive during the winter than at other seasons (Table 2). A greater proportion of males than females were reproductive during the winter ($\chi 2 = 28.253$, $P < 0.01$ (Table 3). Proportion reproductive males and females was highest during the spring in all three habitats (Table 3). Increase in proportion of reproductive males began two months earlier than that of females (January and March, respectively; Table 2). Females continued to display indications of reproductive activity, including pregnancy and lactation, approximately three months longer than did males, July and October, respectively (Table 2).

Amplitudes of population fluctuations

There was no correlation between January-March population densities (see above) and peak densities for the year (bluegrass, $r = 0.227$, $n = 25$, $P = 0.250$; alfalfa, $r = -0.030$ $n = 23$, $P = 0.890$; tallgrass, $r = 0.065$, $n = 24$, $P = 0.763$). Sample sizes were adequate for comparisons of survival and proportion reproductive during April-August with peak densities only in bluegrass. Survival was positively correlated with peak densities ($r = 0.562$, $n = 25$, $P = 0.003$). Proportion of reproductive males and females, combined, was not correlated with peak densities ($r = -0.207$, $n = 19$, $P = 0.395$). When controlling for proportion males and females, combined, that were reproductive, survival remained significantly correlated with peak densities ($r = 0.6057$, $n = 16$, $P = 0.008$).

Precipitation the previous September-December was not correlated with peak densities of B. brevicauda (bluegrass: $r = 0.043$, $n = 25$, $P = 0.838$; alfalfa: $r = 0.174$, $n = 25$, $P = 0.407$; tallgrass: $r = -0.069$, $n = 25$, $P = 0.743$). Nor was April-August precipitation correlated with peak densities in alfalfa ($r = 0.287$, $n = 25$, $P = 0.164$); however, correlations between peak densities and April-August precipitation in bluegrass and tallgrass were significant($r = 0.401$, $n = 25$, $P = 0.047$ and $r = 0.458$, $n = 25$, $P = 0.021$, respectively).

Mean monthly survival, April-August, in bluegrass was not correlated with total precipitation during these months ($r = -0.018$, $n = 25$, $P = 0.933$). Total precipitation the previous September-December was not positively correlated with proportion of reproductive shrews ($r = -0.453$, $n = 19$, $P = 0.051$). Neither was there a correlation between April-August precipitation and proportion reproductive shrews in bluegrass ($r = 0.161$ $n = 19$, $P = 0.511$).

Mean population densities of neither prairie voles nor meadow voles, nor of total vole densities, during April-August were correlated with peak B. brevicauda densities for the year in any of the three habitats (alfalfa: M. ochrogaster, $r = -0.344$, $n = 25$, $P = 0.092$; M. pennsylvanicus, $r = -0.017$, $n = 25$, $P = 0.935$; total voles, $r = –0.072$, $n = 24$, $P = 0.738$; bluegrass: M. ochrogaster, $r = 0.207$, $n = 25$, $P = 0.321$; M. pennsylvanicus, $r = 0.133$, $n = 25$, $P = 0.528$; total voles, $r = 0.222$, $n = 25$, $P = 0.286$; tallgrass: M. ochrogaster, $r = 0.111$, $n = 25$, $P = 0.598$; M. pennsylvanicus, $r = -0.094$, $n = 25$, $P = 0.654$; total voles, $r = -0.40$, $n = 24$, $P = 0.259$).

Survival during April-August was not correlated with mean vole densities during these months (M. ochrogaster: $r = -0.006$, $n = 19$, $P = 0.980$; M. pennsylvanicus: $r = -0.429$, $n = 19$, $P = 0,067$; total voles: $r = 0.430$, $n = 19$, $P = 0.073$). Reproduction was negatively correlated with population density of M. ochrogaster during April-August ($r = -0.488$, $n = 19$, $P = 0.034$); reproduction was not correlated with densities of M. pennsylvanicus ($r = 0.008$, $n = 19$, $P = 0.973$) or total vole densities ($r = -0.293$, $n = 19$, $P = 0.224$).

Partial correlation analyses of peak densities in bluegrass, with precipitation, survival, reproduction, and vole densities were made, while holding the other two factors constant. Only survival was correlated with peak densities (precipitation: $r = 0.418$, $n = 14$, $P = 0.107$; survival: r

= 0.625, n = 14, P = 0.010; reproduction: r = 0.139, n = 14, P = 0.608; vole densities: r = -0.023, n = 14, P = 0.993).

Discussion

Population densities and amplitudes of fluctuation of Blarina brevicauda varied among bluegrass, tallgrass, and alfalfa habitats, with generally higher densities in bluegrass. Variation in survival among the three habitats was the primary factor responsible for higher population densities of B. brevicauda in bluegrass. Differential protection from predators provided by vegetative cover most likely explains variation in survival among habitats. Lin and Batzli (1995) list 21 common predators in our study areas (8 mammalian, 8 avian and 5 snakes). Of these, 3 mammalian predators (least weasel, Mustela nivalis, long-tailed weasel, M. frenata, and mink, M. vison) and all the snakes feed below the vegetation. The remaining predators feed from above the vegetation.

Vegetative cover, including a mat of dead grasses at the surface, was dense year-round in bluegrass, while cover was relatively sparse in alfalfa during all seasons, and especially so in winter. Although vegetative cover was present year-round in tallgrass, there was considerable open space up to 10 cm above the surface in most places. In bluegrass, B. brevicauda would be protected from predators hunting from above (large mammals, raptors and owls) and at the surface (mink, weasels and snakes); weasels and snakes would be restricted mainly to hunting within vole surface runways. In tallgrass, there would be protection from predators hunting from above, but less protection from those hunting at the surface. Both groups of predators would be less impeded while hunting in alfalfa than in the other two habitats. Differences in reproduction among the three habitats, as indicated by proportion of reproductive males and females, appeared to be less important than differential survival in generating higher population densities of B. brevicauda in bluegrass than in the other two habitats. Proportionately fewer reproductive males and females in tallgrass than in alfalfa and bluegrass, however, may have contributed to lower population densities in tallgrass than in the latter two habitats.

Blarina brevicauda displayed annual population fluctuations, with peak densities during early summer-early autumn, in all three habitats throughout the 25 years of the study. These observations are consistent with several prior accounts of demography of Blarina brevicauda (Harper 1929, Blair 1948, Manville 1949, Grant 1979), but differ from those of Lima et al. (2002) who found long-term erratic fluctuations. Although an important factor in among-habitat differences in population density and peak densities, differential survival did not appear to be responsible for generating annual population fluctuations of B. brevicauda. There was no seasonal pattern to survival in the three habitats.

Seasonal variation in reproduction, coinciding with the annual population fluctuations of B. brevicauda, appears to drive annual population fluctuations in this species. However, factors responsible for seasonality in reproduction were not obvious. For example, precipitation was not seasonal in our study region (Records of the Illinois State Water Survey Will). Further, food availability did not appear to be involved in the late summer-early autumn decline in reproduction; insect and other invertebrate populations remain high until at least the first autumn frost (Metcalf and Metcalf 1993). In east-central Illinois, the mean date of first frost is 14 October; reproduction of B. brevicauda at our study sites began to decline before this date. Trapping sessions in this study normally were completed during the first half of each month. The main decline in the proportion of reproductive females occurred between mid September and early October, before the typical date of the first frost. Low food availability could, of course, be a factor in the low level of reproduction during winter. Declines in reproduction also were not related to low temperature stresses; reproduction began declining in June (males) and September (females), well before late autumn temperature declines (Records of the Illinois State Water Survey). Wayne and Rissman (1990) and Chang et al. (1999) indicated that reproductive activation of male house shrews, Suncus murinus, was controlled, in part, by photoperiod. Churchfield (1990) also suggested reproduction in shrews to be related to photoperiod. Because of small monthly sample sizes, we were unable to test for specific effects of photoperiod on reproduction.

Although seasonal variation in reproduction appeared responsible for the annual population fluctuations, reproduction was not involved in differences in peak densities. Variation in mortality appeared to be the most likely factor responsible for variation in peak densities among years. April-August mean monthly survival, but not reproduction, was positively correlated with peak

densities in bluegrass (the only habitat for which sample sizes were adequate for analysis). Lima et al. (2002) also concluded that variation in survival was more important than variation in reproduction in explaining population fluctuations of B. brevicauda. These authors suggested that such changes were intrinsic, and did not address the role of predation in survival.

We found no evidence to support the suggestion by Smith et al. (1974) that precipitation the previous autumn impacted B. brevicauda population densities the following year. Precipitation from April-August and peak densities of B. brevicauda were correlated in bluegrass and tallgrass, but not alfalfa. We suggest that lesser cover in alfalfa, and higher mortality from predation, offset the influence of precipitation in this habitat. The dense mat of dead vegetation over the surface in bluegrass and tallgrass also may have resulted in more moist conditions than in the open alfalfa. Getz (1965, 1971) found, however, that although relative humidities were higher where vegetative cover was denser, absolute humidities did not differ; the latter are more important than relative humidities in respiratory water balance of small mammals (Getz 1968). Mattlock et al. (2002) suggested that greater numbers of Blarina hylophaga in areas of dense vegetative cover may have involved greater food availability as a result of more moist soil and air conditions. Pankakoski (1985) also suggested that breeding success of Sorex araneus was promoted by improved food availability from high precipitation during the breeding season.

While variation in precipitation was positively associated with peak densities in bluegrass and tallgrass, neither survival nor reproduction was correlated with precipitation. Partial correlation analysis of effects among precipitation, reproduction, and survival revealed that only survival was correlated with peak densities. During an extreme drought, June-September 1988, survival rates were > 30% lower than the 25-year mean for these months (Getz 1994). Reproduction, on the other hand, was not adversely affected by the drought

If B. brevicauda is a major predator on adult or nestling voles, then B. brevicauda densities should have been high when vole densities were high owing to increased food availability. Population densities of neither species of vole during the period of annual population growth of B. brevicauda (April-August) were correlated with peak densities of B. brevicauda for that year in any habitat. That neither survival nor reproduction of shrews during April-August was correlated with population densities of voles during this period further suggests that predation on voles was not a major factor influencing population densities of B. brevicauda.

Observations during the course of a study of social organization of M. ochrogaster (Getz et al. 1993) support the conclusion that B. brevicauda is not a major predator on nestling M. ochrogaster. In that study, we trapped directly at the nests of M. ochrogaster. Blarina brevicauda seldom were captured at nests occupied by voles, even when numbers of B. brevicauda were high in the site and individuals were captured in traps set away from vole nests. Only after voles abandoned a nest did we capture B. brevicauda at vole nests. Direct observations under seminatural laboratory conditions of interactions between B. brevicauda and family groups of voles indicate that shrews rarely prey on nestling prairie voles, but do prey on nestling meadow voles (Getz et al. 1992).

We conclude that seasonal reproduction was the major factor involved in generating annual population fluctuations of B. brevicauda, but not in variation in peak densities among years. Differential mortality, most likely from predators, appeared to be the primary factor responsible for variation in annual peak densities. Analyses of vole population fluctuations indicated varying assemblages of predators were responsible for erratic high-amplitude fluctuations of both M. ochrogaster and M. pennsylvanicus in our study sites (Getz et al. In Prep). Because B. brevicauda populations fluctuate annually, we suggest that B. brevicauda experienced predation effects different from those of the voles, and that such differential survival did not drive annual population fluctuations of this species.

Similar conclusions regarding effects of predators on shrews have been drawn from studies of Fennoscandian shrews (Skaren 1972; Hansson 1984; Kaikusalo and Hanski 1985 Henttonen 1985; Korpimaki 1986; Sonerud 1988; Henttonen, et al. 1989; Korpinmaki and Norrdahl 1989). Shrew populations in Fennoscandia, especially those of Sorex araneus, displayed erratic seasonal fluctuations that typically were not in synchrony with cyclic fluctuations of voles. Non synchronous high population densities of voles and shrews, but synchronous declines in numbers of voles and shrews suggest that predators switch from voles to shrews as densities of the former decline. In controlled experiments, Norrdahl and Korpimaki (2000) found that vole-eating

predators depressed alternate prey populations, including shrews. Summer declines in low-density shrew populations synchronous with declines in vole populations in Lapland, also suggest a common causal agent, most likely predation by weasels (Henttonen, et al. 1989). That some high density shrew populations in eastern and western Finland displayed only modest declines in numbers during periods of high vole densities indicates regionally different predator assemblages are involved in the dynamics of shrew populations.

Getz (1994) discusses the potential impact of predation by mammals, birds and snakes on population fluctuations of B. brevicauda, based on analysis of the first 18 years of this study. He concluded that varying effects of generalist avian, mammalian and snake predators were involved in differential mortality of B. brevicauda among habitats. Such predation did not appear to be responsible for generating annual population fluctuations. However, the combined impact of several generalist predators, populations of each controlled by different factors, is presumed to be responsible for variation in annual population fluctuations within and among habitats.

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Table 1. Mean monthly survival (proportion of animals present that month surviving to the next month) of Blarina brevicauda, 1972-1997. Data for males and females combined. Sample sizes in parentheses.

Month	Bluegrass	Alfalfa	Tallgrass
January	0.518 (191)	0.306 (36)	0.288 (66)
February	0.436 (179)	0.217 (23)	0.452 (31)
March	0.548 (135)	0.474 (19)	0.346 (26)
April	0.461 (217)	0.263 (38)	0.400 (25)
May	0.395 (362)	0.266 (94)	0.358 (53)
June	0.437 (535)	0.306 (180)	0.415 (65)
July	0.493 (673)	0.391 (197)	0.505 (101)
August	0.528 (685)	0.432 (229)	0.549 (142)
September	0.488 (642)	0.450 (198)	0.399 (183)
October	0.473 (584)	0.282 (220)	0.373 (201)
November	0.395 (539)	0.284 (116)	0.366 (153)
December	0.414 (324)	0.300 (60)	0.308 (91)

Table 2. Total monthly proportion of Blarina brevicauda reproductive during 1972-1997. Data from all three habitats combined. Sample sizes in parentheses.

Month	Males	Females
January	0.367 (30)	0.074 (68)
February	0.739 (37)	0.061 (33)
March	0.938 (16)	0.765 (17)
April	0.871 (31)	0.767 (43)
May	0.846 (91)	0.827 (104)
June	0.607 (112)	0.752 (169)
July	0.422(121)	0.586 (151)
August	0.275 (91)	0.515 (134)
September	0.378 (90)	0.471 (121)
October	0.250 (165)	0.265 (223)
November	0.175 (206)	0.116 (198)
December	0.079 (76)	0.083 (120)

Table 3. Total seasonal proportion of Blarina brevicauda reproductive during 1972-1997. Sample sizes in parentheses. Values with different superscripts within columns are significantly different at 0.05 level, Tukey's HSD test).

Season	Males			Females	
	Bluegrass	Alfalfa	Tallgrass	Bluegrass	Alfalfa
Spring	0.858a (113)	0.824a (17)	1.000a (8)	0.757a (111)	0.933a (30)
Summer	0.457a (223)	0.480a (50)	0.353ab (51)	0.597a (355)	0.719ab (64)
Autumn	0.246a (228)	0.257a (109)	0.218b (124)	0.259ab (301)	0.287ab (108)
Winter	0.361a (97)	0.316a (19)	0.111b (27)	0.092b (141)	0.074b (27)
Total	0.439 (661)	0.369 (195)	0.267 (210)	0.426 (908)	0.467 (229)
F; df	2.639; 3,8	2,088; 3,8	6.173; 3,8	5.582; 3,8	25.102; 3,8
P	0.131	0.180	0.018	0.023	<0.001

Fig. 1. Population densities (number/ha) of Blarina brevicauda in three habitats in east-central Illinois. Data represent monthly mean population densities of all study sites in each habitat for 1972-1997.
Fig. 2. The pattern of fluctuation of Blarina brevicauda populations in three habitat in east-central Illinois. Data represent monthly mean (+ SE) population densities from all study sites in each habitat for 1972-1997.
Fig. 3. Survival of Blarina brevicauda following first capture in three habitats. Sample sizes in parentheses.